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Trinidadian guppies use a social heuristic that can support cooperation among non-kin

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Short title: Social heuristics and real-world cooperation

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Abstract

Cooperation among non-kin is well documented in humans and widespread in non-human animals, but explaining the occurrence of cooperation in the absence of inclusive fitness benefits has proven a significant challenge. Current theoretical explanations converge on a single point: co-operators can prevail when they cluster in social space. However, we know very little about the real-world mechanisms that drive such clustering, particularly in systems where cognitive limitations make it unlikely that mechanisms such as score keeping and reputation are at play. Here we show that Trinidadian guppies (*Poecilia reticulata*) use a ‘Walk Away’ strategy, a simple social heuristic by which assortment by cooperativeness can come about among mobile agents. Guppies cooperate during predator inspection and we found that when experiencing defection in this context, individuals prefer to move to a new social environment, despite having no prior information about this new social group. Our results provide evidence in non-human animals that individuals use a simple social partner updating strategy in response to defection, supporting theoretical work applying heuristics to understanding the proximate mechanisms underpinning the evolution of cooperation among non-kin.

Introduction

The conundrum of cooperation [1, 2], where one individual pays a cost so that another can receive a benefit, was highlighted by Darwin [3], who realised that individuals that express a trait (e.g., cooperation) must themselves benefit for the trait to be favoured by natural selection. Yet cooperation is seen at every level of biological organization (intra cellular to societal) [4] and across taxonomic groups from microbes to humans [1]. Cooperation becomes particularly difficult to explain when benefits are conferred upon unrelated individuals and the past three decades have seen substantial theoretical attention given to identifying pathways by which non-kin cooperation can evolve (e.g. direct reciprocity [5], indirect reciprocity [6], generalised reciprocity [7-9], network reciprocity [10], group selection [11] and by-product benefits [12]). The merits of each of these models have been much debated [13-17], but they all have a single unifying feature: for cooperation to persist, co-operating individuals must cluster together [reviewed in 18]. Essentially, cooperation can prevail when cooperative individuals interact at higher rates with each other than with non-cooperative individuals, because this decreases the exploitation of cooperators by defectors and increases reciprocation of cooperative benefits to cooperators. Thus clusters of co-operators can gain higher fitness payoffs than defectors in the population [19, 20]. Identifying the processes that drive the clustering of cooperation in social landscapes is thus at the heart of unravelling the conundrum of how costly behaviours that benefit non-kin have evolved [19].

Theoretical work suggests that heuristics, simple decision-making rules, can underpin social dynamics (the formation and breaking of social ties) and thereby drive assortment by cooperation [18, 21-23]. For example, decisions about joining or leaving groups in response

to cooperation or defection can generate social assortment by individual cooperativeness (i.e. phenotypic propensity to cooperate) [18, 22-24]. Heuristics incorporate behavioural rules for making fast and economical decisions when the information available to individuals is incomplete and the future is uncertain [25]. These conditions for decision making are likely to be prevalent in systems with noisy, rapidly varying social environments and where decision making is not supported by advanced cognitive abilities; conditions which typify many non-human social animals. Currently however, it is unclear whether heuristics have a role to play in driving the dynamical linking of social ties in non-human animals in the context of cooperation. This represents a key gap in understanding cooperation, as characterizing the behavioural rules that govern dynamical linking is fundamental to determining the mechanisms that drive the clustering of co-operators [26]. Here we probe the social heuristics that underpin the formation and breaking of social ties in the context of cooperation in Trinidadian guppies (*Poecilia reticulata*).

Trinidadian guppies live in dynamic fission-fusion societies where individuals cooperate with non-kin during predator inspection [27] and where there is evidence of social assortment by cooperative tendency [28]. During predator inspection in fish, one or more individuals will leave the shoal to approach the predator closely and gain information about the level of threat posed by the predator [29]; information that benefits all members of the group [30]. Work in guppies and other fish species has demonstrated that inspectors pay a personal cost of increased risk of predation [31, 32], which they can reduce by inspecting in cooperative partnerships [33-35]. There has been much debate on the mechanisms maintaining cooperation during predator inspection, with some evidence suggesting a ‘TIT-for-TAT’ strategy is used [36]. In this strategy, individuals initially cooperate with a partner and in future, repeated iterations with this same partner, copy the partner’s last move (i.e. either

cooperate or defect) [36]. Given the highly dynamic nature of daily social interactions however, and the large number of individuals that make up each individual's social environment [37, 38], guppies are also likely to rely on simple behavioural mechanisms of assortment that will allow them to avoid having to process and store the high volumes and rates of social information that they are exposed to. Guppies therefore constitute a potentially powerful model system for a new avenue of empirical work to test for key assortment mechanisms proposed by theoretical models to underpin the evolution of cooperation among unrelated individuals.

We aimed to test whether individuals use a simple behavioural strategy - 'leave in the face of defection' requiring only limited information on the behavioural tendencies of others. Models by Aktipis [18, 22] and Schuessler [24] show that such simple heuristics can generate assortment among cooperative mobile agents. Under a 'Walk Away' conditional movement strategy, individuals break away from defecting social partners [18, 22-24] and join a new partner or group upon encounter, without information on the behavioural tendencies of the partner or group [18, 22]. The conceptual attraction of the 'Walk Away' heuristic for generating positive assortment of cooperative phenotypes in real-world populations is that it avoids cognitively demanding bookkeeping. That is, it does not require committing to memory the identity of social partners, or indeed their behaviour over multiple iterations, to aid in making decisions to associate with a partner (or partners). This is in contrast to the TIT-for-TAT strategy, which requires remembering the last actions of specific partners (i.e. partner behaviour and identity). The strategy also differs from other exit strategies such as the well-known 'win-stay, lose-shift', where an actor continues or "stays" with an action – cooperate or defect - unless the gain no longer meets some threshold and then switches or "shifts" to the opposing action - cooperate or defect in an iterated game [39]. Like with a

‘TIT-for-TAT’ strategy, an individual thus changes their own cooperativeness as a reaction to that of others [although for an approach that models ‘win-stay, lose-shift’ with ‘shift’ including an option to leave the group see 23]. In contrast, in the ‘Walk Away’ strategy individuals in effect change their social environment without any prescription for who to join or how to behave (cooperate or defect) in any subsequent round or game [18, 22, 24]. That is, with a ‘Walk Away’ strategy, individuals do not need to be able to exhibit plasticity in their own cooperative behaviour, further contributing to its simplicity and, importantly, possible traits under selection [e.g., 40, 41-43].

‘Walk Away’ models for the evolution of cooperation were originally formulated for populations with fairly stable group structures [18, 22, 24]. However, populations of social animals typically live in societies with fission-fusion dynamics, such as those experienced by Trinidadian guppies. It is not immediately clear that under these conditions, a ‘Walk Away’ strategy can allow positive assortment of cooperation to emerge against the background merging and splitting of groups, which in this and other systems is driven by myriad factors [44]. We have therefore confirmed that a ‘Walk Away’ social heuristic can generate assortment by cooperation in populations with fission-fusion dynamics similar to those in guppies using an agent-based simulation model to further support the rationale for the current study (see supplementary materials). To test the hypothesis that guppies will use a ‘Walk Away’ strategy, we exposed individuals to unfamiliar social partners, manipulated their perception of these partners’ cooperative behaviour during a predator inspection event and then monitored the propensity for individuals to change their social environment following their ostensible experience of cooperation or defection. We predicted that if a ‘Walk Away’ strategy exists in this species, individuals would prefer to associate with novel social partners over social partners that they had just experienced defection from.

Methods

Study animals

We used laboratory reared adult female Trinidadian guppies descended from wild fish collected in the lower reaches of the Aripo River (10°40' N 61° 14' W) on the island of Trinidad, a site where adult guppies experience a high risk of predation from piscivorous fish. Focal fish were housed in groups of 10 in 29 x 19 x 17 cm aquaria. Stimulus fish were housed in groups of 100 in 80 x 30 x 39 cm aquaria. Focal and stimulus fish were randomly selected from stocks of fish housed under naturalistic conditions in four physically isolated pools (approximately 2000 fish per pool). All fish were fed twice daily to satiation on their specified diet (stimulus fish diets are explained below; focal fish were fed on a diet of tropical fish flake and brine shrimp, *Artemia* sp.). The study was carried out under UK Home Office Licence PIL 30/8944, reviewed by the University of Exeter Animal Welfare and Ethical Review Body, and in strict accordance with the UK Animals (Scientific Procedures) Act 1986. To minimize stress, all fish used in the study were provided with plant refugia and always had, at a minimum, visual access to social partners, with the exception of our control experiment where focal fish were without contact to social partners during testing. Power analysis after an initial data collection phase (N=6 replicates per cell) was used to ensure that we used the smallest number of animals possible while maintaining high test power (16 replicates per cell, SPSS SamplePower 21 v. 3.0.1, IBM SPSS Inc.).

Experimental apparatus and procedure

Study design

To test for the existence of a ‘Walk Away’ strategy in Trinidadian guppies, we experimentally exposed 136 female guppies to a cooperative or non-cooperative social environment and subsequently tested their social preference for ostensibly the same social environment versus a novel one.

Predator inspection

Inspection arenas were similar to those used in other studies involving predator inspection in guppies (e.g., [28, 45, 46]). Aquaria (80 x 30 cm) were sub-divided with Perspex partitions to produce two inspection lanes and two predator enclosures (Fig. 1A). A guide system was in place between the predator enclosures and the inspection lanes where a removable opaque partition was positioned to visually isolate the predator enclosure from focal fish prior to the start of a trial. Predator enclosures were either empty or contained a single predatory fish (*Aequidens pulcher*) depending on condition (see below). A refuge was located at the end opposite to the predator enclosures with an artificial plant and a perforated transparent rectangular stimulus shoal compartment (10 x 4.5 x 18 cm). The inside of each inspection lane was lined with a reversible partition that had a mirror on one side and a uniform, light grey surface on the other side. With this design, in a mirrored lane an inspecting fish was ostensibly joined by a fish from the compartment of social partners (i.e. the stimulus shoal) in the form of its mirrored reflection, and in a non-mirrored lane also connected to a compartment of physically constrained social partners an inspecting fish ostensibly experienced defection from these partners (Fig. 1A). This experimental paradigm built on protocols used in previous studies [reviewed in 47], and recent work has illustrated that using a mirror stimulus in a predator inspection context elicits behaviour in a focal fish that aligns with its behaviour with a live partner [28]. The water depth in each subsection of an arena

was 11 cm. Arenas were illuminated with full spectrum 40W bulbs and filmed from above using Samsung digital colour cameras (Model: SCB-2001) fitted with a Computar 5-50mm, F1:1.3 lens.

Thirty minutes before the onset of each trial, predator naïve stimulus shoals were placed in the stimulus shoal compartments of each inspection lane. Each stimulus shoal consisted of four size-matched, predator-naïve female guppies that the focal fish had not previously encountered. We manipulated identity cues of the stimulus shoals by feeding them on one of two diets (larval *Chironominae* sp. or adult *Daphnia* sp.) that were novel to the focal fish, for min. 7 days and up to 14 days prior to the trials. Guppies use odour cues for social decision making [48] and this method allowed us to generate distinct novel odour cues for groups of fish. Stimulus shoal compartment walls were perforated to allow odour cues to diffuse across the compartment barrier. During their inspection of the predator (Fig. 1A) focal fish could thus become familiar with global (shoal level) odour cues of social partners originating from their diet in tandem with experiencing either defection or cooperation, depending on treatment.

At the start of a trial, individual focal fish were released into the centre of an inspection lane and allowed 10 minutes to acclimatize. During this period the opaque partition between the predator enclosures and the inspection lanes remained in place. Focal individuals were then gently encouraged into the refuge area next to the confined stimulus shoal using a dip net. The opaque partition between the predator enclosures and inspection lanes was then lifted. In experimental test trials the lifting of the barrier revealed a live predator and in control trials, intended to account for possible effects inherent to the experimental setup, an empty enclosure. Inspection occurred when fish left the refuge area and swam towards the predator

enclosure. Mirrored lanes simulated cooperation by a member of the stimulus shoal, while non-mirrored lanes simulated defection by all members of the shoal. Trials ended after a 5-minute inspection period and focal fish were immediately removed from the inspection lane and transferred in a small container of water into a binary choice tank for the social partner choice test (see below). At the end of a trial all stimulus fish were removed and a complete water change of the arena was carried out.

Social partner choice test

Immediately following the predator inspection trial, focal individuals were transferred to a binary shoal choice arena and tested for their association preferences for social partners fed either on the same diet as experienced in the predator inspection trial (i.e. *Chironominae* sp. or *Daphnia* sp. fed fish) or the unfamiliar (novel) diet. Arenas (45 x 30 cm, water depth 11cm) were sub-divided into three compartments using perforated Perspex barriers similar to [49]. Two stimulus shoal compartments at opposite ends of the arena measured 7.5 x 30 cm, which left a middle compartment for the focal fish that measured 30 x 30 cm. Arenas were illuminated and filmed as above. Forty-five minutes prior to the onset of a trial a shoal of 5 fish was placed in each stimulus shoal compartment of the choice arena (matched for body size across shoals). One compartment contained fish on the *Daphnia* sp. diet and the other contained fish on the bloodworm diet. Each focal fish was thus presented with one stimulus shoal composed of fish on the same diet as the fish they had experienced in the inspection trial and another composed of fish on the second novel diet, to which the focal was naïve. All stimulus fish were predator naïve and had not been used in the predator exposure treatment. This design was used because the experiences of the stimulus fish during the inspection trials could potentially lead to differential behaviour between the two shoals during the choice trial

if they were used there as well. Using odours as identity cues allowed us to avoid this potentially confounding factor. At the start of a choice trial, focal fish that had just been removed from an inspection trial were placed in the centre of the arena and given 5 minutes to acclimatize. After acclimatization, we recorded the time that focals spent shoaling with each stimulus shoal over a 10-minute period. Focal fish were recorded as shoaling with stimulus fish if they were within 5 cm of the barrier to a shoal compartment (preference zone; based on the elective group size concept [50]). At the end of the trial all fish were removed from the arena and a complete water change was carried out.

Analysis of behavioural data

Our analysis is based on 129 focal fish that entered the preference zone of both shoals at least once during the shoal choice trial (7 fish did not visit both sides; Supplementary material Table S1). The inspection and shoaling behaviour of each focal fish was scored manually using the Observer XT v. 10.1 by a single observer (SKD) blind to the condition and treatment that focal fish were in. For inspection trials we quantified the average distance of focal fish to the predator enclosure over the 5-minute inspection period. For shoal choice trials we calculated the proportion of shoaling time that focal fish spent with each of the two shoals which were angular transformed prior to statistical analysis as per convention for analysing proportional data in this way [51].

We used a general linear model (GLM) to test for effects of our experimental manipulations on the social partner choices made by our focal fish. In the model we used the angular transformed proportion of time spent with the novel (unfamiliar odour) shoal during the binary shoal choice trial as the dependent variable, and condition (2 levels: control and

experimental), social experience (2 levels: defection and cooperation) and stimulus shoal diet encountered during inspection (2 levels: *Daphnia* and bloodworm) as fixed effects..Our initial model contained the inspection behaviour of our focal fish as a covariate, however it had no effect ($F_{1,116}=0.393$; $p=0.532$, see Supplementary materials Table S2)) and was removed from the final model. We explored a significant interaction between condition and treatment using *post hoc* one-sample t-tests with a Bonferroni corrected α level of 0.0125.

Methods of non-social control experiment

We ran a non-social control experiment that used a modified version of the main experimental paradigm in order to investigate whether any effects found in the main experiment could alternatively be explained by the guppies connecting their experience (cooperation/defection) with the odour cues themselves, rather than with the social environments associated with those odour cues. That is, effects found in the main experiment could potentially be explained by a mechanism that caused focal individuals to, for example, avoid an odour that they associated with high predation risk in the defection condition (approaching a predator as a singleton). In this control experiment, the overall design was the same as in the main experiment (inspection then shoal choice) and odour cues derived from the same diets were used (*Chironominae* sp. and *Daphnia* sp.; see below)), but no social cues (no stimulus shoal and no mirror) were provided in the inspection trials. In the subsequent shoal choice test, focal individuals could choose between two shoals of fish, each of which was paired with one of the two odours.

Odour cues in this experiment were introduced in the form of odour water. This was created by masticating frozen daphnia or bloodworm (*Daphnia* sp., and *Chironominae* sp., i.e. the

same diet odours as in the main experiment) in water (5 g of daphnia and 2.6 g of bloodworm per 300 ml water) and filtering the mixture through a fine sieve in order to remove macroscopic particles. The odour water was introduced into the predator inspection lane at the refuge end, where the stimulus shoal was placed in the main experiment (opposite to the predator stimulus end), via a plastic tube connected to a funnel placed over the tank. The rate at which the odour water entered the tank was controlled by a flowmeter (MMA-35, Dwyer Instruments, Michigan City, IN, USA) set to 25 ml/min. 500ml odour water was placed in the funnel prior to the trial and the flowmeter was opened at the beginning of the trial. The trial otherwise proceeded as in the main experiment (as per above in a ‘no mirror’ condition only). The subsequent binary shoal choice tests were also similar to the ones in the main experiment; except that the stimulus shoals each consisted of four females that had not been fed with the diets used to create odours. Instead, odour water (200 ml) with the two experimental odours was introduced into each shoal compartment prior to the test trial, one odour in each compartment. The experimental tanks were thoroughly cleaned after each trial to remove any odour remains. We used a one-sample t-test to test for a preference for shoals paired with the novel odour, taken as the angular transformation of the proportion of shoaling time spent with this shoal.

Results

We found that the presence or absence of a predator during the inspection portion of a trial (i.e. inspection condition: experimental or control) interacted with having partners that either cooperated or defected during the inspection (i.e. social experience: cooperation or defection) to influence subsequent shoal choice (Table 1). *Post hoc* analysis revealed that individuals experiencing a defecting social environment preferred partners with an unfamiliar odour over

partners with a familiar odour when given a subsequent choice (Fig. 1B), which was not the case for control treatments (no predator) or our experimental cooperation treatment, where we did not find any preferences (Table 2, Bonferroni corrected $\alpha=0.0125$).

If the significant preference found in the main experiment was based on avoidance of the odour associated with inspecting a predator as a singleton, rather than avoidance of the social environment associated with the predator inspection experience, then a preference for a shoal bearing a novel odour (as opposed to that experienced during inspection), should also be present in the non-social control experiment. However, in this control experiment we found that focal fish did not show a preference for fish associated with the novel odour (back-transformed mean proportion of time spent with novel odour fish \pm SE = 0.448 ± 0.0406 / -0.0403 ; $t_{62} = -1.275$, $p = 0.2070$).

Discussion

We found that female Trinidadian guppies experiencing a social environment where all others defected during predator inspection, preferred novel partners (that they had no prior information on) over ostensibly familiar social partners in a subsequent social choice test. This result demonstrates that individuals actively sever ties with defecting social partners and seek out links with others, even when they do not have information on the cooperative behaviour of these novel social partners; both are consistent with a ‘Walk Away’ strategy [18, 22, 24]. To our knowledge this is the first empirical evidence for the existence of this social heuristic in a non-human animal system.

In humans the option to leave a defecting partner, ‘opting out’, has been shown both theoretically and empirically to allow cooperation to prevail [52-56] and empirical work suggests that something akin to conditional movement strategies is active in humans. For example, dynamic partner updating under conditions of limited information has been demonstrated experimentally in response to low levels of cooperative behaviour in partners [40, 52, 54, 55, 57]. Indeed, one study has shown that when constrained to a set behavioural repertoire of either staying with an interaction partner or joining another, randomly assigned, partner between rounds of a cooperative game, movement (‘link-breaking’) decisions generate assortment of cooperative behaviour across a network of interaction partners [40]. It is important to note that in the majority of paradigms in these empirical studies with humans, participants operate with partner-specific information that goes beyond what is outlined for a ‘Walk Away’ strategy, so that ties are preferentially broken with defectors and new ties are preferentially made with co-operators [e.g., 52, 57] or individuals are able to log the behaviour of specific individuals and use this knowledge in subsequent encounters with those individuals [40]. Still, at the core of these paradigms, having knowledge of and control over the option to leave is critical in determining the economic decisions made by players [52, 54, 55, 58, 59], even when the assignment of a new partner is made at random [54, 55, 59]. Our study provides evidence of the existence of this class of strategies outside of humans and supports its simplest use, with individuals making social association choices when they have no information on the value of future partners. The simplicity of this strategy means that it may be widespread in natural systems [60]. Furthermore, future work examining the heritability of the ‘Walk Away’ strategy and how it has been shaped by natural selection would provide valuable insights into the evolution of cooperation in natural populations.

Although our findings highlight a mechanism that may go some way to explaining the persistence of non-kin cooperation in guppy populations, they do not preclude other mechanisms that may be working simultaneously in this species; such as choosing specific partners based on immediate observation of their cooperative tendency [e.g., 61, but see below] or conditional cooperative behaviour based on the cooperative behaviour of current social partners [10, 62-64]. For example, generalized reciprocity (or ‘help anyone if helped by someone’), has been demonstrated with computer modelling to generate positive assortment of cooperative interactions via cooperative responses conditional to experience [65]. Support for cooperation via generalized reciprocity is based on experiences of cooperative behaviour that is wholly anonymous (i.e. identification of the actor is not necessary), and thus may be particularly relevant for the guppy system [23,65-66]. Future work exploring if other social heuristics are used in combination with a ‘Walk Away’ strategy to support cooperation in guppies is eagerly anticipated.

In our experiment, in addition to guppies ‘walking away’ from defecting partners it could also be expected that they would prefer the social environment where they had experienced cooperation. Both of these would work toward driving the positive assortment by cooperative propensity [reviewed in 67 and see Supplementary materials Section 1] that we have seen evidence for in wild guppy populations [28]. We did not, however, find clear evidence that our focal individuals preferred partners that had cooperated during predator inspection over partners for whom they had no information on their propensity to cooperate. Previous evidence from this study system indeed suggests that individuals have a preference for a more cooperative over a less cooperative partner when given a choice between the two [61]. . However, a key paradigm difference between the experiment presented here and this previous work [61] is that individuals were able to choose from social partners for whom they had

complete information; that is, they had knowledge of the cooperative propensity of each potential partner in a binary choice test. This means that although fish may have been actively choosing the more cooperative partner, they may alternatively have been actively choosing to leave the defecting partner as in our study. In support of this latter explanation, we can consider evidence from work in humans suggesting a higher propensity to remember traits or experiences associated with defectors compared to cooperators [68]. In humans this effect appears to be linked to the importance of the information in predicting trait characteristics of individuals and thus the outcome of future interactions [69, 70]. In this case, a negativity bias can exist when ‘negative’ cues are more diagnostic than ‘positive’ cues [70]. With a ‘Walk Away’ heuristic, the important diagnostic information regarding the behaviour of an unfamiliar social group is whether they defect during predator inspection, as opposed to whether they cooperate, as this is what drives the decision to leave. It could be that the underlying premise for this strategy is a negativity bias, particularly when an entire group of individuals defects compared to when just one individual from a group cooperates (i.e. the diagnostic value of the ‘positive’ information is low). An increased propensity to remember social partners from a situation where they defected, but not where they cooperated, and then acting on this information for subsequent social association decisions, thus seem like plausible explanations for the updating behaviour and lack of preference for cooperative shoals that we observed.

Theoretical work over the last decade has striven to identify simple behavioural mechanisms that can maintain cooperation among non-kin [most recently reviewed in 63, 67, 71], with social heuristics likely being important drivers in systems with high levels of social mixing [e.g., 72]. In our experimental design, individuals did not have the opportunity to use individual recognition or other information when making partner choices. The work we

present thus truly represents evidence of a real-world heuristic for dynamical linking of social ties in non-human animals. It most closely resembles a ‘Walk Away’ heuristic, which can generate positive social assortment by cooperative behaviour in populations of mobile agents ([18] and see Supplementary materials Section 1). The simplicity of this strategy means that it may be a general mechanism contributing to the maintenance of cooperation across a broad range of taxa where individuals can detect non-cooperative behaviour, but where more complex processes involving, for example, intent and knowledge attribution or bookkeeping of behaviour [73-76], are not necessarily present. We look forward to further developments in this area.

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Ethics

The study was carried out under UK Home Office Licence PIL 30/8944, reviewed by the University of Exeter Animal Welfare and Ethical Review Body, and in strict accordance with the UK Animals (Scientific Procedures) Act 1986.

Data, code and materials

Data: <http://hdl.handle.net/10871/18463>

Competing interests

The authors declare no competing interests.

Authors' contributions

The main empirical study was conceived and designed by SKD and DPC and data collection overseen by SKD. The empirical validation study was designed and carried out by JBB in discussion with SKD. The simulation model was conceptualized by SKD, RJ and DPC, designed by RJ and implemented by JC. SKD wrote the first draft of the manuscript in discussion with DPC. All authors contributed to subsequent revisions. SKD and DPC designed and produced the figures in discussion with RJ.

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Figure legend

Figure 1. (A) Predator inspection arena with illustrative examples of movement of fish in inspection lanes (red lines) (B) When focal fish had experienced defection by a shoal during predator inspection they differed from other groups in a social partner choice paradigm. They showed a preference for novel social partners over social partners that were ostensibly from the shoal they had experienced while inspecting a predator (control = condition with no predator present; **=significant at $\alpha=0.0125$; error bars= ± 1 SEM).

Table 1. Results of the analysis of the main experiment testing for an effect of the inspection condition that fish were in (no predator present, i.e. control, versus predator present, i.e. experimental), the social environment that fish experienced during the inspection portion of a trial (cooperative vs. non-cooperative), the type of diet (daphnia or bloodworm) that novel shoaling partners had been fed on and their interactions. The significant interaction between inspection condition and social experience was further explored (Table 2). The significant effect of diet type was driven by an overall preference for fish that had been fed on a bloodworm diet.

Source	<i>F</i> (1,121)	<i>p</i>
Inspection condition	0.294	0.589
Social experience	5.491	0.021
Diet type	4.549	0.035
Inspection condition * Social experience	6.134	0.015
Inspection condition * Diet type	0.000	0.984
Social experience * Diet type	2.840	0.095
Inspection condition * Social experience * Diet type	0.062	0.804

Table 2. Results of the *post hoc* t-tests of significant interaction terms in the behavioural dataset (see Table 1). Significance after Bonferroni-correction ($\alpha=0.0125$) is shown in bold and indicates a preference in the shoal-choice experiment for a novel social environment after individuals have experienced defection.

Inspection condition	Social experience	t	df	p
No predator present	Cooperation	0.377	29	0.709
	Defection	0.353	32	0.726
Predator present	Cooperation	-1.675	32	0.104
	Defection	2.933	32	0.006